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Microbial communities and carbon cycling in subglacial ecosystems and their analogues

Mikrobiální komunity a koloběh uhlíku v subglaciálních ekosystémech a jejich analogie

Bachelor thesis

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Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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Abstract

Subglacial environments are located at the interface of glacier ice and bedrock. They represent one of the major ecosystems associated with glaciers and ice sheets. They contain liquid water and fine material including organic matter, accumulated during periods of glacier advance. It is well established that there are active microbial communities residing in these environments, which are adapted to living in extreme conditions. Subglacial ecosystems are mostly isolated from the atmosphere and thus their oxygen content is usually very low. Therefore, the organisms residing in these environments often employ anaerobic/anoxic strategies to ensure their survival. However, knowledge of these communities is limited due to practical constrains associated with subglacial ecology and biogeochemistry research. The activity of microorganisms beneath glaciers significantly influences carbon cycling. In recent years, this ecosystem is dynamically changing and may have important impact on regional and global carbon cycle. Therefore, it is important to better understand this ecosystem. This thesis summarizes recent knowledge of microbial communities and carbon cycling in this ecosystem and discusses suitable analogues, which could help us understand the fascinating subglacial ecosystem and formulate future research questions.

Key words: subglacial environment, glaciers and ice sheets, microbial activity, organic matter, carbon cycling

Abstrakt

Subglaciální prostředí se nachází na rozhraní ledovců a jejich podloží. Představuje jeden z hlavních ekosystémů spojených s ledovci a ledovcovými pokrývkami. Zahrnuje tekutou vodu i jemný materiál rozdrcený pohybem ledovců obsahující organický uhlík. Je dobře známo, že v něm existují aktivní mikrobiální komunity, které obývají toto prostředí a jsou přizpůsobeny životu v extrémních podmínkách. Jelikož jsou subglaciální ekosystémy většinou izolovány od atmosféry, obsah kyslíku je tu obvykle velmi nízký, proto organismy obývající tato prostředí často používají anaerobní/anoxické strategie k zajištění svého přežití. Znalosti týkající se subglaciálních ekosystémů jsou velmi sporé především kvůli praktickým omezením, která znesnadňují výzkum subglaciální ekologie a biogeochemie. Aktivita mikroorganismů pod ledovci výrazně ovlivňuje koloběh uhlíku. V posledních letech se zmíněný ekosystém dynamicky mění a může mít výrazný vliv na regionální a globální koloběh uhlíku. Z tohoto důvodu je lepší pochopení probíhajících procesů velmi důležité. Předložená práce shrnuje současné poznatky o mikrobiálních komunitách a koloběhu uhlíku v tomto ekosystému. Dále se zabývá vhodnými analogy, které by mohly pomoci v chápání fascinujícího subglaciálního ekosystému, a v neposlední řadě se pokouší formulovat otázky pro příští výzkum.

Klíčová slova: subglaciální prostředí, ledovce, mikrobiální aktivita, organický materiál, koloběh uhlíku

Contents

Introduction

The subglacial environment comprises the interface of glaciers and ice sheets and their bedrock and represents one of the major ecosystems associated with glaciers (Wadham et al. 2004). It belongs to the cryosphere, the portion of the Earth where water is present in its solid form. Therefore, in the subglacial environment, important ecological functions are maintained by microorganisms adapted to low temperatures (Margesin & Miteva 2011).

More than 10% of the surface of the planet Earth is covered by ice. Even though the extent of Earth's surface cover by ice during the last glacial maximum is subject to debate, it is considered to have been at least three times that of present-day coverage (Clark et al. 2009). Despite the large area of glaciers at present and in the past, microbial communities and their functions in subglacial systems have not been sufficiently described and understood. Nevertheless, it is known that these microbial communities play significant roles in carbon cycling, as well as that of other elements. Increasing attention has been paid to biogeochemical processes in the subglacial environment due to their possible global impacts (Wadham et al. 2008). However, due to practical challenges associated with subglacial research, there is still not enough information to form a full picture of the workings of the subglacial ecosystem.

Aims

The main aim of this thesis is to summarize the current knowledge of the subglacial ecosystem, especially that of the microbial communities and their role in carbon cycling.

Our knowledge about life beneath glaciers and changes associated with their melting is far from complete and many questions remain unanswered. Therefore one of the aims of this work is to find suitable analogues of the subglacial ecosystem, for which more knowledge and information are available. Reviewing the knowledge of microbial diversity and interaction with the physical conditions of these analogues could help us understand the fascinating subglacial ecosystem and help us focus on future research questions.

1. Subglacial ecosystem characteristics

This chapter focuses on the current knowledge of subglacial ecosystems. It reviews the life limiting-factors of the subglacial environment, such as low temperature and water and nutrient availability. In addition, the process of carbon cycling is described, including the degradation of organic carbon compounds and their fate in the environment. For the comprehensive understanding of subglacial systems it is also necessary to describe the biodiversity of microbial communities in the subglacial environment.

1.1. Life limits

Microorganisms inhabiting subglacial environments are facing severe challenges of how to deal with the extreme physical conditions of the environment they reside in. They have evolved different ways of accommodating to it and a range of adaptations related to metabolic processes. Apart from the low temperature, subglacial microorganisms have to resist desiccation and frequent nutrient limitation problem (Cavicchioli et al. 2002).

1.1.1. Low temperature

A significant portion of planet Earth is permanently exposed to temperatures below 5 °C. Low-temperature environments are found in the deep sea, snow, permafrost, sea ice, glaciers and ice sheets. These environments are successfully colonized by microorganisms called psychrophilic or psychrotolerant. These organisms are able to survive and even thrive at low temperatures.

Psychrophiles have several adaptations particularly suited for low temperature, which can complement each other (Margesin & Miteva 2011). An important factor to be considered for living in cold environment is the fluidity of cell membrane. Low temperatures cause its rigidity and therefore reduced functionality. The problem is resolved by an increase in the proportion of unsaturated fatty acids and a decrease in the average fatty acid chain length (Metz et al. 2001). Anti-freezing proteins are another example of creativity of these extremophiles. Some bacteria produce anti-freezing proteins as one of the ways of how to endure and thrive in cold environment, to avoid cell freezing and to reduce destructive effects of ice crystallization. It helps them to be functional even in these extreme life conditions (Gilbert et al. 2005). Another adaptation is the synthesis of cold-adapted enzymes. These enzymes increase flexibility of cells and allow them to be highly active at low temperatures (Siddiqui & Cavicchioli 2006).

1.1.2. Liquid water

Availability of liquid water is a key factor for organisms living at low temperatures. It can be supplied to and become available for microorganisms in subglacial systems in several ways. Surface meltwater can descend through moulins and crevasses in the glacier to the basal zone. The water can then accumulate at the glaciers bed (Fig. 1) (Fountain & Walder 1998, Hodson et al. 2008).

Figure 1 - Subglacial outflow (photo: Jakub Žárský)

Glacier ice is an excellent thermal insulator and the heat generated at the glacier bed is primarily used to warm the basal ice and so to generate liquid water. The two main heat sources are viscous heat dissipation due to vertical shearing and friction at the glacier base, and geothermal heat originating from within the Earth (Veen et al. 2007).

A significant amount of subglacial lakes can be found under the ice sheets. Beneath the Antarctic ice sheet, more than 300 subglacial lakes have been discovered (Wright & Siegert 2011). Hence, there is a possibility of extensive drainage system, since many of them are thought to be warm-based (Bell 2008). One of the most well-known and most investigated lakes is Lake Vostok lying beneath the Antarctic ice sheet (250 km in length, up to 50 km wide and >500 m deep). Water drainage system could also have occurred beneath the Greenland ice sheet (Fig. 1) (Lindbäck et al. 2015). However, the scope of this thesis is limited to the information of water-rock-ice interface of glaciers and ice sheets.

1.2. Energy and nutrient sources

Figure 2 - The front of a glacier (terminus) containing basal layers of subglacial material (photo: Jakub Žárský)

The interface between rock and ice contains fine debris created by the physical weathering of rock covered by glaciers or ice sheets. These remains consist of various types of minerals and organic carbon, which can serve as potential sources of energy and nutrients.

The principal source of carbon for the subglacial ecosystem is organic matter overridden during periods of glacier advance (Fig. 2). However, only a small proportion of subglacial organic carbon is labile and so readily available for microorganisms. For example, it is well known that soil organic matter consists of at least three pools, including first, relatively simple soluble organic molecules and second, relatively labile polymers such as hemicellulose and non-lignified cellulose (which can be anaerobically degraded). The third pool, lignin and lignified cellulose, is the least degradable substrate (Miyajima et al. 1997). Boreal forest and tundra ecosystems were overridden by ice sheets during the last glaciation and probably contain all these types of organic substrate (Trumbore 2000).

Nitrogen required for microbial metabolic activity in subglacial environments is mostly obtained by mineralization of organic nitrogen from overridden organic matter, with subsequent oxidation of released ammonium (NH_4^+) to NO_3^- (Wynn et al. 2007). Phosphorus is present in the Earth's crust in the form of PO_4^{3-}. Glacial erosion predominantly leads to phosphorus yields and subsequently to release for microbial needs. (Hodson et al. 2005). The combination of carbon, nutrient and liquid water availability makes subglacial sediments suitable place for microbial life (Wadham et al. 2004, Tranter et al. 2005, Bhatia et al. 2006).

A wide range of metabolic processes occur in subglacial environments. First, chemolithoautotrophy has been detected in sampled subglacial environments. Chemolithotrophic organisms generate energy through the oxidation of reduced inorganic compounds and utilize CO_2 as the sole carbon source for growth and thus may form the base of the subglacial food web (Boyd et al. 2014, Christner et al. 2014). Second, (chemo)heterotrophy is widespread in subglacial environments. Heterotrophs use organic compounds as their carbon source and obtain energy through the oxidation of these compounds. Their source organic carbon can be derived from chemolithoautotrophic production, or they can use ancient organic matter from the sediments overridden during glacier advance (Mikucki et al. 2009).

Bedrock composition has a significant effect on the redox chemistry and microbial metabolic activity (Skidmore et al. 2005). Aerobic chemolithoautotrophs and heterotrophs consume oxygen derived from meltwater, which originates from basal ice in the subglacial environment. When all available oxygen has been depleted, alternative electron acceptors become crucial for metabolic processes, and various strategies may be implemented by the present microorganisms (Wadham et al. 2004, Tranter et al. 2005). Nitrate and sulphate reduction can be used as energetic reactions (anaerobic respiration) in subglacial environments. Both of these processes have been measured in sampled sediments (Boyd et al. 2011, Skidmore et al. 2000). Another type of microbial activity in anoxic conditions is Fe(III) reduction, with Fe(III) serving as the terminal electron acceptor (Mikucki et al. 2009). Fermentative metabolisms have also been identified, promoted by the presence of a suitable organic carbon substrate and an absence of higher-energy-yielding electron acceptors (such as O_2 and SO_4^{2-}) with which to degrade organic matter (Dieser et al. 2014). Organic compounds, such as fatty acids, alcohols and others, can be converted by various bacteria to acetate, carbon dioxide, hydrogen, and perhaps formate. These compounds can are subsequently be used as substrates by the methanogens (Schink 1997).

Methanogenesis, the biogenic production of methane, is one of the end-member reactions of carbon cycling in the subglacial ecosystem (see section 1.3) (Boyd et al. 2010, Wadham et al. 2008). Methanogenic microorganisms can either oxidise hydrogen with CO_2 (hydrogenotrophic methanogenesis) or acetate (acetoclastic methanogenesis) to generate energy and acquire carbon.

1.3. Carbon cycling

The sources of organic carbon mentioned in previous chapter are used by microorganisms in the subglacial environment. They can contain e.g. n-alkanoic acids, steroids and other functionalized compounds typical of old microbial (cyanobacterial and algal) and plant material (Stibal et al. 2012b). These types of carbonaceous material are easily biodegradable by microbes (Skidmore 2000). Recalcitrant organic compounds, such as cellulose or lignin, which are also present in subglacial environments (see section 1.2), can also potentially be degraded by microorganisms; however, no evidence for these processes has been found to date.

Organic matter degradation is a complex process. Often, products of one set of reactions are used as substrates in other reactions. Organic carbon is oxidized by aerobic or anaerobic respiration, depending on the available terminal electron acceptors, or it can be disproportionated during fermentative processes (Fig. 3). Final products of these reactions can subsequently be used by methanogens. However, very little information exists about these intermediate processes in the subglacial ecosystem.

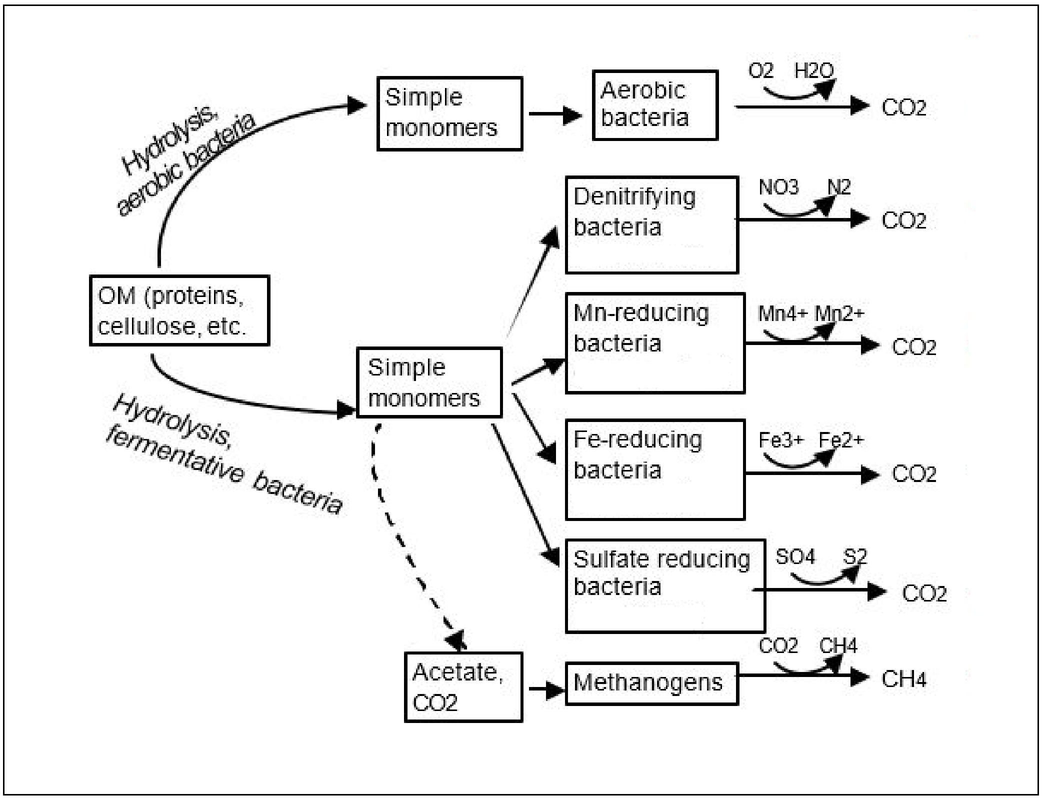

Figure 3 - The sequence of redox processes involved in mineralization of organic substances (source: Internet)

The production of methane seems to be the last step for organic matter degradation in the subglacial ecosystem (Wadham et al. 2008). Methanogens are a very diverse group of microorganisms, yet they can consume only a limited number of substrates. There are three main types of substrates they can use: CO_2, methyl-group containing compounds, and acetate. Therefore it is clear that methanogens depend on non-methanogenic organisms for their survival.

The life of methanogens is influenced by the type of substrates they utilize. The primary type of substrate is CO_2. Most methanogens are hydrogenotrophs that can reduce CO_2 to methane using H_2 as the primary electron donor:

$$4\,H_2 + CO_2 \rightarrow CH_4 + 2\,H_2O$$

Many hydrogenotrophic methanogens can also use formate as their main electron donor. The second type of methanogens is using substrates from methyl-group containing compounds, such as methanol, methylated amines (monomethylamine, dimethylamine, trimethylamine, and tetramethylammonium), and methylated sulfides (methanethiol and dimethylsulfide). Finally, acetoclastic methanogens use acetate as their substrate. Acetate is the most abundant intermediate compound in the anaerobic food chain, and the major part of biologically generated methane can be derived from acetate (Liu & Whitman 2008):

$$CH_3COOH \rightarrow CH_4 + CO_2$$

Methanogenic archaea are important producers of methane and therefore play a unique role as active components of the Earth atmospheric system and global carbon cycling (Wadham et al. 2008). By examining samples collected from various locations, it has so far been shown that methanogens occur in various subglacial environments (Boyd et al. 2010, Stibal et al. 2012b). Therefore further research on this type of ecosystems necessary to increase our knowledge on these life forms pivotal for carbon circulation in our atmosphere.

Wherever oxygen is present methanotrophic aerobic bacteria use methane as a carbon and energy source and they remain an essential component of many natural ecosystems, in particular in areas where methane is produced and subsequently consumed. Therefore methanotrophic bacteria influence the level of atmospheric methane and play a key role in the overall cycle of methane on Earth (Hanson & Hanson, 1996). They occur most frequently on the boundary of aerobic and anaerobic environments in wet areas (Sundh et al. 1994). Methanotrophic bacteria often act as a biofilter for diffusing methane from anaerobic zones. Thereby, they reduce and control the potential leakage of methane into the atmosphere. Methanotrophs have been identified in meltwaters flowing out of subglacial environments (Dieser et al. 2014), but their role in subglacial ecosystem is still unclear.

Methane can also be oxidised anaerobically by a particular group of Euryarchaeota. Anaerobic oxidation of methane could also occur subglacially, in which case the amount of potential release of methane from beneath glaciers and ice sheets could be significantly lower. An analogy to such conditions is sea-bed sediment where anaerobic oxidation of methane is responsible for 90% of methane oxidation. Archaea capable of anaerobic oxidation of methane (known as anaerobic oxidisers of methane) cooperate with syntrophic bacteria that use sulfate (or NO_3^-, Fe^{3+}) as the final electron acceptor (Knittel & Boetius 2009).

1.4. Microbial diversity

In the past it was believed that the environment beneath glaciers is not inhabited (Raiswell 1984). However, it became evident that it is a suitable environment for activity at the microbial level (Sharp et al. 1999, Skidmore et al. 2000).

Subglacial environment is heterogeneous and geochemically diverse, because of the variety of environments that existed before glaciation. Physical and chemical factors determine the conditions of life and therefore the composition of microbial communities. These factors are diverse and specific to each different subglacial environment.

The abundance of bacteria and archaea is usually between 10^3–10^5 cells per ml of sediment in the basal zone of subglacial systems (Anesio & Laybourn-Parry 2012). Proteobacteria, Actinobacteria, and Bacteroidetes are usually the dominant groups identified in subglacial samples. For example, samples collected from the Bench Glacier showed Betaproteobacteria to be dominant, followed by Alphaproteobacteria, Gammaproteobacteria, Deltaproteobacteria and Epsilonproteobacteria (Skidmore et al. 2005). Proteobacteria were also highly represented in the John Evans Glacier, mostly represented by Betaproteobacteria, Alphaproteobacteria and Gammaproteobacteria. Actinobacteria and Bacteroidetes were also found in John Evans Glacier sediments (Skidmore et al. 2005). The basal ice from two temperate New Zealand glaciers contained cultivable Proteobacteria and Bacteroidetes (Foght et al. 2004). Proteobacteria were also dominant in beneath Robertson Glacier, together with Actinobacteria (Mitchell et al. 2013). Sampling of sediments from Lower Wright Glacier in Antarctica and Russell Glacier in Greenland has revealed similar results, with Proteobacteria again dominant. Most of them were Gammaproteobacteria or Betaproteobacteria, followed by other groups, such as Firmicutes and Acidobacteria (Stibal et al. 2012a). The West Antarctic ice Sheet has also been sampled. Microbial communities of this subglacial environment were represented by Betaproteobacteria, Alphaproteobacteria and Actinobacteria (Lanoil et al. 2009). These bacterial groups have a wide range of metabolic diversity including different respiration pathways or fermentation. However, it is still not clear what exactly they are doing due to the lack of specific information.

Archaea have also been found in subglacial environments. Methanogenic archaea of the euryarchaeal order of Methanosarcinales have been detected in samples from Robertson Glacier in Canada (Boyd et al. 2010). Beneath the Russell Glacier in Greenland organisms from the euryarchaeal orders of Methanosarcines and Methanomicrobiales were found (Dieser et al. 2014). Measurements have confirmed that methanogenic archaea are active members of the microbial communities in subglacial sediment samples from Lower Wright Glacier and Russell Glacier. Methanomicrobiales and Methanosarcinales were identified in these locations (Stibal et al. 2012b). Another example of archaeal groups found in the subglacial environment is ammonia-oxidizing archaea (Boyd et al. 2011).

2. Subglacial ecosystem analogues

This chapter discusses the potential subglacial ecosystem analogues such as permafrost and subseafloor sediments. Even though these analogues are not identical with subglacial systems in all particular characteristics, they can be similar in specific features which can help us understand the subglacial environment. Comparing them with subglacial environments will help us formulate questions which can be useful in the subsequent subglacial ecology and biogeochemistry research.

2.1. Permafrost

Permafrost is traditionally defined as soil that has remained frozen (that is, below 0 °C) for at least 2 years (Jansson & Taş 2014). Permafrost could be a suitable analogue of the subglacial ecosystem due to its similarity in organic matter sources and their processing. The fate of organic carbon in permafrost has been intensively studied and the knowledge of degradation processes the wide range of organic carbon substrates and of the microbes involved in them could be applied to the subglacial ecosystem.

The top layer of permafrost, called the active layer, is exposed to freezing and melting cycles during the season. The thickness of the active layer is variable and, owing to global warming, it has been increasing (Walter et al. 2006, Vieira et al. 2010, Koven et al. 2011). The active layer can be thick enough not to completely refreeze in winter: this is how talik is formed (Yoshikawa & Hinzman 2003). During the winter permafrost bursts and thermal contraction cracks occur. They can be filled by meltwater during the summer season. The following winter the cracks form into ice wedges by refreezing of water inside them. Expansion within ice wedges affects creation of polygons. These polygons can occur in the Arctic and Antarctica (Raffi & Stenni 2011, Morse & Burn 2013). Several types of landscape features can be identified in permafrost, containing unfrozen layers. These are also influenced by the ongoing temperature changes. These features are called cryopegs. Their freezing point is depressed owing to high concentration of dissolved solids in the pore water (Gilichinsky et al. 2005). Thawing of ice-rich permafrost and massive ground ice cause that the surface is inundated and thermokarst lakes are forming. These lakes are also known as thaw lakes. Their formation is possible due to low-drainage soil system (Brouchkov et al. 2004). All these permafrost features could be considered analogues of subglacial sediments being exposed to the atmosphere upon deglaciation and the various geomorphological processes associated with glacial retreat.

2.1.1. Life limits

As in the subglacial ecosystem, microorganisms living in permafrost are often classified as psychrophiles, since they are able to grow and reproduce at low temperatures (Feller & Gerday 2003). The lowest temperature at which microbial activity has been measured is -17 °C (Panikov et al. 2006). Very similar to the subglacial environment, microorganisms in permafrost have evolved several strategies for survival and thriving at subzero temperatures. They have adaptations such as regulation of membrane fluidity by modifying lipid composition of their membranes. Other adaptations are the same as those that the microorganisms living in the subglacial environment have evolved. In general these adaptation strategies are similar in all low-temperature environments. Their other adaptations include cold-adapted proteins that improve their structural mobility at low temperatures, cold-shock, antifreeze proteins and others (Biasi et al. 2005, Vatsurina et al. 2008, Suetin et al. 2009). One of their main strategies is the dormant state with low metabolic activity (D'amico et al. 2006).

In addition to temperature, water availability is an important factor for microbial biomass, their diversity and the structure of their community. In cold ecosystems, microbial activity and associated nutrient cycles are driven primarily by water availability and secondarily by nutrient availability (Zeglin et al. 2009).

2.1.2. Life strategies

The composition of the microbial community reflects the unique and extreme conditions of the permafrost environment. Permafrost is estimated to contain around 15% of the world's soil carbon, much of which is frozen as poorly decomposed plant remains (Post et al. 1982). In consideration for specific conditions one should point out that permafrost contains diverse range of organisms, which have key role in carbon cycling. For example, they are able to decompose recalcitrant organic carbon compounds including cellulose, lignin, chitin and other complex carbon compounds (Wagner et al. 2009, Yergeau et al. 2010).

Permafrost also contains nutrients, which are limited by a diffusion barrier formed at different levels, depending on the temperature that limits metabolic activity (Rivkina et al. 2000).

There is a wide diversity of bacterial life strategies present in permafrost. Wherever oxygen is available, aerobic bacteria are present (Trotsenko & Khmelenina 2005). However, permafrost is a very heterogeneous environment, with a high proportion of anaerobic habitats, which is why other strategies may become dominant. Arctic and Antarctic permafrost contains microbial diversity from different functional guilds, including denitrifiers, iron reducers and sulphate reducers (Palmer & Horn 2012, Rivkina et al. 1998). Methanogenesis as an important microbial process in carbon cycling is also present. In particular, acetoclastic methanogens and hydrogenotrophic methanogens play key roles in these processes (Mondav et al. 2014). Finally, methanotrophic bacteria have also been detected (Rivkina et al. 1998, Trotsenko & Khmelenina 2005).

2.1.3. Permafrost microbial ecology and climate change

The microbial ecology of permafrost has recently become center of increasing attention due to the impact of its thawing and microbial degradation of trapped organic matter. Upon processing, this organic matter to be released as one of the greenhouse gases, such as CO_2, CH_4 or N_2O. The total amount of organic carbon in permafrost has been estimated to be 1,672 Pg (Tarnocai et al. 2009), which is approximately equal to the total amount in vegetation and the atmosphere. As the permafrost thaws, organic carbon is more available for microorganisms and therefore their metabolic activity increases, which could further yield to the greenhouse gas effect (Mackelprang et al. 2011, Graham et al. 2012).

However, the long-term consequences of permafrost thawing are not well understood. Samples from Holocene and Pleistocene permafrost contained between 0.6% and 12.4% organic carbon. It has been shown that model simulations of aerobic and anaerobic CO_2 and CH_4 production over 100 years predicted lower carbon emissions than those that are currently estimated (Knoblauch et al. 2013).

During thawing, both methane and CO_2 are released. The initial burst of methane is considered to have mainly been due to the release of trapped gas from the frozen permafrost. Much of the methane has subsequently been consumed by methanotrophic bacteria. This example highlights the importance of understanding the sources and sinks of greenhouse gases in a warming climate (Graham et al. 2012), and can present an interesting analogue to the subglacial ecosystem, where greenhouse gases may also be trapped in significant amounts (Wadham et al., 2012).

2.1.4. Microbial habitat

Significant numbers of viable ancient microorganisms are known to be present within the permafrost. These bacteria are good material for research of microbial evolution and low temperature adaptation, as they possess mechanisms which allow them viability for long periods of time. Because of depth and heterogeneity of permafrost one could assume that this habitat is home of various microbial communities (Gilichinsky et al. 2008).

There are different types and yet specific conditions of both ice and soil within the permafrost. Such variability can create a wide range of diversity and composition of microorganisms within them. The cell abundance in different permafrost types can vary considerably, whereby cell counts could range from 10^5–10^8 per gram of dry mass (Gilichinsky et al. 2008), which is higher than those in subglacial environments.

The majority of microorganisms isolated from buried permafrost are bacteria, although fungi, algae and Archaea have also been found (Gilichinsky et al. 1995). Bacterial diversity of Arctic permafrost has been investigated from different locations. Most common groups of collected samples were Proteobacteria, Firmicutes, Acidobacteria, Actinobacteria and Bacteriodetes (Steven et al. 2007, Yegreau et al. 2010, Wihelm et al. 2012, Taş et al. 2014,). Antarctic permafrost has also been subject of research. Most abundant groups of this locality were Acidobacteria, Actinobacteria, Proteobacteria, Bacteroidetes, Firmicutes and Cyanobacteria (Smith et al. 2006, Blanco et al. 2012, Stomeo et al. 2012). In addition to these specimens, a wide diversity of methanotrophic bacteria occurs in permafrost, such as *Methylomicrobium* spp. and *Methylobacter* spp. (Rivkina et al. 1998, Trotsenko & Khmelenina 2005).

Archaea have also been detected in permafrost. One of such important groups of organisms is methanogenic archaea, which highly influence carbon cycle and are represented by Methanomicrobiaceae, Methanosarcinaceae and Methanosaetaceae (Morozova & Wagner 2007, Ganzert et al. 2007).

2.2. Subseafloor sediments

This analogue was chosen for analysis not only for its permanently cold environment, but mainly due to the stratification of the sediments with respect to their redox conditions and microbial communities. Considering this analogue could be helpful for the understanding of microbial activity in the subglacial ecosystems and its dependence on redox conditions.

A significant part of the seafloor is permanently cold with temperatures below 4°C and it is also inhabited by psychrophilic microorganisms (Knoblauch et al. 1999). Marine sediments are created by process of accumulation of particles that sink to the seafloor from the overlying water column. The thickness of this layer is variable (Ryan et al. 2009). Features and composition of sediments, as well as microbial communities depend on various factors, such as the origin of the deposited material, as well as sediment particle size which has a significant impact on the porosity of sediments and ultimately affects fluid and chemical transport in sediments. Microorganisms can use material substrates that are either deposited with the sediment or diffuse into it from the overlying seawater or underlying crust. The most important substrate for them is organic matter which is deposited, degraded and remineralized. Rates of remineralization depend on both the quantity and quality of organic matter (Hedges et al. 1988, Niggemann et al. 2007). Availability of terminal electron acceptors determines the rate of organic matter remineralization. As the seawater circulates through the oceanic crust, sediments are transfered from midocean ridges. This change could cause sediments containing oxygen, nitrate and sulfate to diffuse upwards from the crust. Furthermore, these sediments also include terminal electron acceptors which are available for organisms (Orcutt et al. 2011).

2.2.1. Metabolic reactions

One of the principal factors controlling microbial activity in subseafloor sediments is the redox potential and the available terminal electron acceptors. Their presence controls the rate of organic carbon remineralization. This could be a useful analogy to the less researched subglacial ecosystems where redox potential gradients also likely occur. Subseafloor sediments are well stratified in well-defined zones (Orcutt et al. 2011). Since oxygen which is found in top layers of sediments is quickly depleted, other terminal electron acceptors have become important. Nitrate, manganese and iron reduction occur but sulphate reduction is the quantitatively most significant organic matter remineralization process (Thamdrup & Canfield 1996, Berner 1978, Reeburgh 1983). Due to the organic matter degradation to carbon and depletion of other available terminal electron acceptors, microbial methanogenesis from bicarbonate and hydrogen occurs, leading to the accumulation of significant amounts of methane (Floodgate & Judd 1992). It is estimated that about 10% of total organic matter is converted into methane by methanogenesis (Claypool & Kvenvolden 1983). However, methane diffuses upwards to the sulfate zone and it is consumed by anaerobic oxidisers of methane by the process of sulfate reduction (Iversen & Blackburn 1981, Thomsen et al. 2001).

2.2.2. Microbial diversity

There is a high variability in the abundance of cells in subseafloor sediments due to factors such as depth of sediments and distance from organic carbon sources. Cell densities in sediments range from 10^6 to 10^9 per cm^3 (Parkes et al. 2000, D'Hondt et al. 2002, D'Hondt et al. 2009). Top oxygen-rich surficial layers are occupied by bacterial communities from the Alphaproteobacteria, Deltaproteobacteria and Gammaproteobacteria, Acidobacteria, Actinobacteria and Planctomycetes. Archeal diversity in these layers is low (Bowman & McCuaig 2003). Deep sediments support bacterial communities mainly Chloroflexi, Proteobacteria and archaeal communities, such as Methanosarcinales and Methanobacteriales (Inagaki et al. 2006, Inagaki et al. 2003, Kormas et al. 2003, Newberry et al. 2004, Parkes et al. 2005).

3. Comparison of the subglacial ecosystem and its analogues

This chapter summarizes the similarities between the subglacial ecosystem and the described analogues, focusing on the aspects which have not been sufficiently described in the subglacial ecosystems. The main point of interest is carbon cycling and the fate of carbon in the ecosystem.

Permafrost is a useful analogue ecosystem as it contains similar recalcitrant organic substrates. Metabolic pathways and carbon cycling processes similar to those in permafrost are also likely to occur in subglacial environments. Thus, if microorganisms that are responsible for the degradation of organic substrates in permafrost also occur in subglacial sediments, it could be a sign of these processes also taking place under glaciers. However, it is questionable if the magnitude of methane is same or lower beneath glaciers as estimates for permafrost. After glacial retreat this trapped greenhouse gas could be released to the atmosphere with possible ecological impact.

While permafrost may be similar to subglacial environments in terms of organic substrate types, subseafloor sediments could represent a useful analogue due to the possible similarity in redox potential gradients and the fact that subglacial and marine ecosystems are often connected. The fact that methane accumulated in subseafloor sediments can be consumed by anaerobic oxidisers of methane is indicative of a potential for similar process in subglacial sediments with analogous redox gradients. The amount of methane available for release to the atmosphere upon glacier retreat could be lower than estimated previously if this process is active under glaciers. However, the rates of anaerobic oxidation of methane depend on the presence of suitable terminal electron acceptors and, as these are not as plentiful as in the subseafloor sediments, are likely to be much lower in the subglacial environment.

Conclusions and outlook

The understanding of the subglacial ecosystem is far from complete despite the increasing interest and the amount of works about the subglacial environments.

Subglacial environments are a potential reservoir of methane, which can be released into the atmosphere as a consequence of glacial melting and retreat (Wadham et al. 2012). However, if anaerobic oxidation of methane occurs in subglacial environments, the amount of methane that can potentially be released into the atmosphere would be significantly lowered, analogous to sea-bed sediments where anaerobic oxidation of methane is responsible for up to 90% of methane oxidation. Microbes capable of anaerobic oxidation of methane (anaerobic oxidisers of methane) have been found in subglacial sediments, and there is preliminary evidence that anaerobic oxidation of methane occurs when there is sufficient amount of SO_4^{2-}, e.g. when subglacial sediment is export to a fjord. Currently, it is not known if anaerobic oxidation of methane can occur in the subglacial environment where SO_4^{2-} concentrations are low.

Therefore, future research could be focused on long-term incubation experiments with subglacial sediment and studying the potential for anaerobic oxidation of methane in the subglacial environment and its large-scale impacts.

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